

The embryology and development of *Riccia*
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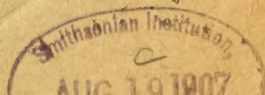
DEPARTMENT OF BOTANY

The Embryology and Development
of *Riccia Lutescens* and
Riccia Crystallina

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THE EMBRYOLOGY AND DEVELOPMENT OF *RICCIA* *LUTESCENS* AND *RICCIA* *CRYSTALLINA*.¹

CHARLES E. LEWIS.

(WITH PLATES V-IX)

IN June 1903, while collecting liverworts in the vicinity of Ithaca, N. Y., an abundance of material of *Riccia lutescens* was found growing around the edges of dried-up ponds. In some cases the plants formed beautiful rosettes, but usually they grew in irregular clusters, often being so closely crowded together as to cover the ground for several square centimeters.

The individual plants vary greatly in shape and size. The younger light green plants consist of a narrow, thin, ribbon-shaped thallus which has a longitudinal median groove. In the older plants the fore part of the thallus is thickened, very large air cavities being formed. The thallus is attached to the soil by numerous rhizoids from the older part, the apical end being free. On the under side are numerous colorless lamellae.

As the fruiting plant is unknown there is doubt as to the relationship of this species, authorities differing widely as to its status. LINDBERG (21) claimed that it was merely a sterile terrestrial form of *Ricciocarpus natans*. UNDERWOOD (30) says of it: "approaches certain terrestrial forms of *Ricciocarpus natans*, and possibly derived from that species, but better kept distinct." STEPHANI (28) states that it is probably not a *Riccia* but a sterile marchantiaceous hepatic.

For the purpose of determining the true relationship of the species, Professor ATKINSON suggested the desirability of following the development of the plant through the summer and autumn, and of securing fruiting specimens if possible. He had found young antheridia in plants collected several years before, but had not traced the development further. It also seemed desirable to study the embryology and cytology of the plant if material could be obtained, because comparatively little has been done on these phases of the life history of *Riccia*.

¹ Contribution no. 106, from the Department of Botany, Cornell University.

BISCHOFF (2) investigated a number of species and settled beyond a doubt the function of the sexual organs. His work was followed the next year by LINDENBERG's monograph (20) which added little that was new.

The study of the development of *Riccia* really begins with HOFMEISTER (15), who gave an account of the development of the thallus, sexual organs, and fruit of *Riccia glauca*.

KNY (19) made a careful study of the apical cells and the method of growth of the thallus. He did not secure plants developing from spores but used delicate thalli which had grown crowded together and did not bear sexual organs in the younger parts, so that the regular order of cells was not disturbed. He discovered the origin and manner of growth of the ventral scales and described the development of the sexual organs. Although HOFMEISTER believed that young antheridia and archegonia could not be distinguished, KNY points out that they are distinct after the first walls are formed.

LEITGEB (22) gives a complete account of the method of growth of the thallus in the Ricciaceae. His study of the sexual organs and fruit was in many cases incomplete on account of insufficient material.

BIOLOGY OF *RICCIA LUTESCENS*.

The account of the biology of *Riccia lutescens* given here is based on field observations extending through two years, together with experiments and observations upon plants kept growing under favorable conditions in the greenhouse and laboratory.

The first observations were made late in June. At that time the plants were growing upon the mud around the edges of ponds. Some of the thalli were very small and delicate, appearing merely as green specks on the mud, while others, which seemed to be older, had the ribbon-shaped form and thickened apical end already described (figs. 1-3).

Material was collected and examined from time to time during the summer and autumn, with the expectation of finding plants bearing the sexual organs, because the statement is usually made that the species of *Riccia* fruit in summer and autumn when growing on the soil. The plants continued to grow well vegetatively throughout the summer, when they were in such a location that they were

supplied with sufficient moisture. In some cases the mud became so dry and hard that the plants were killed, but whenever they were sheltered by a stone or other object, or were growing on the sides of holes, such as cattle tracks, they grew well.

In October all but the youngest and most crowded plants showed the typical *Riccia lutescens* form. At this time young antheridia were found. Material was now collected and fixed from time to time for the purpose of studying the development of the sexual organs. In very few cases were archegonia found in plants collected in autumn. A few young stages were found in plants collected late in November, at which time the older antheridia were almost mature. No further development took place out of doors until spring, because the plants became covered with snow, or with water by the filling up of the ponds, and remained so until April. A quantity of the plants were kept growing on the soil in the greenhouse through the winter, and developed mature sexual organs long before spring. Plants taken from under water in March, just as the ice was going out of the ponds, showed exactly the same form as in November, and little or no further development had taken place. So it seems that the development depends to some extent on temperature, and might be expected to vary with different conditions of climate. A warm winter, in which some growth might take place, would in all probability hasten the development of the sexual organs. Another point of interest is that the submerged plants did not seem to have been injured.

A quantity of material still attached to the soil was taken from under water late in March, and was kept growing in shallow pans in the laboratory so that it could be kept supplied with a sufficient quantity of water for growth but not enough to flood the plants. This was done in order to determine whether the plants would continue the development of sexual organs and fruit in the same way when supplied with a limited amount of water and growing on the soil, as when supplied with a large amount of water which would tend to cause them to break loose and float. It was found that the plants growing on the soil did produce fruit abundantly and at the same time as those growing under natural conditions. The archegonia begin to develop in April in the same thalli which have

produced antheridia, and all stages are found by May 1. About this time fertilization takes place, and by May 25 all stages of sporophyte are found. The arrangement of the sexual organs in the thallus is shown by *figs. 7-11*.

The vegetative growth is very rapid during April and May, the thallus becoming broad and branched by the increase in the number of growing points. The narrow older part by which the thallus is attached decays, and the younger part bearing the sexual organs and sporophytes is set free and floats upon the water. When the plants are supplied with a large amount of water changes take place in the lamellae. They grow to great size and become purple. In the floating thallus decay of the older part continues; the part bearing the antheridia first disappears, then the part bearing the sporophytes, and finally the growing points may be separated, one thallus thus giving rise to several new individuals. In most cases observed the decay of the older parts in floating plants did not advance so far. The plants were carried up around the edge of the pond by the waves, and as the water went down were left stranded upon the mud. When the thalli settle down upon the mud, the large ventral plates wither, and rhizoids are put forth which in a few days attach the thallus to the soil. Growth now continues at the growing points, so that new branches are produced which form rosettes.

When the thallus is injured at this time new plants are immediately produced from the cells of the apical region. This was first observed in plants injured by being covered with mud, in which case slender delicate outgrowths were produced (*fig. 4*). Other plants injured by snails soon developed long slender plants (*fig. 3b*). Thalli were cut into pieces to determine whether other cells would show the same plasticity, but new plants were produced only from cells near the growing point. VÖCHTING (33) found in *Lunularia* that regeneration takes place from cells in various parts of the thallus, but this does not seem to be true of *Riccia natans* under the conditions in which I have studied it. Large numbers of the plants which were left upon the mud when the water went down were injured by cattle coming down to the ponds to drink. Later in the season the cattle tracks were lined with young, green, ribbon-shaped plants

which were outgrowths from the growing points of the older plants. The cattle tracks serve a good purpose, as the young delicate plants are shaded and protected to some extent during the dry season. Two forms of the thallus are produced by the different methods of propagation. In the one case the thallus after it becomes attached to the soil continues its growth, branches and forms a rosette, while in the other case the thallus is injured, and very delicate forms are produced. When large numbers of the floating thalli are deposited near together and are then injured, we find the irregular clusters of plants which have been described in the first paragraph.

The thallus of this plant during the floating period bears such a striking resemblance to *Ricciocarpus natans* that one is led to the conclusion that *Riccia lutescens* is only a ground form of *Ricciocarpus natans*. Since the beginning of this study and after it was well under way, a paper was published by GARBER (II) which dealt with the life history of *Ricciocarpus natans*. Several points in the biology of the plant as given by GARBER differ from those found to obtain at Ithaca, and since the structure of the thallus as well as the embryology is conclusive proof that the two forms are the same species, it seems proper to call attention to these differences and then to give briefly the embryology before taking up the other phases of the study.

The greatest difference in our observations lies in the relation of the supply of water to sexual reproduction. GARBER states that *Ricciocarpus natans* as it grows at Chicago spends its entire life, from the germination of the spore to the production of spores, in the floating state, and that the occasional fruiting plants found upon the soil in summer are plants in which the sexual organs developed and the sporophytes began their development while the plants were floating. He observed no case in which sexual organs were produced on plants growing upon the soil and states that *Ricciocarpus natans* has not yet acquired the power to reproduce sexually when growing upon the soil. The sexual organs develop in April.

The plants at Ithaca, however, spend the greater part of their life upon the soil and only float upon the water for a few weeks at the fruiting period. The sexual organs begin to develop in autumn while the plants are on the soil and plants kept on the soil and sup-

plied with a limited amount of water developed fruit. At the time when the antheridia begin to develop the gametophyte is under favorable conditions for vegetative growth, but is not supplied with an abundance of water. The soil is moist and the conditions are such as would favor the growth of a terrestrial form like *Marchantia*.

The plants seem especially adapted to spend the winter submerged and do not perish under such conditions. The fore part of the thallus contains very large air cavities and thus the tissue is aerated. It is well known that certain higher plants which grow in wet situations have large air spaces in the tissue, and GANONG (12) calls attention to the fact that those marsh plants which are submerged for a portion of the year are able to survive on account of their capacity for air storage. About May 1 the older part of the thallus, which is narrow and thin, has decayed, and the younger parts, bearing the sexual organs, is set free and floats. GARBER points out that when land forms are placed upon the water only a small portion of the apical end remains above the surface, while the older part of the thallus extends into the water and decays. This is true of plants taken from the soil in summer, but in the spring when the free part of the thallus is thick and contains large air cavities, it floats readily. The length of the floating period depends of course upon the conditions of the pond. In some cases the plants may very soon be carried up around the edge of the pond and deposited on the mud, but floating forms are usually found until the ponds are almost dry. In the case of ponds which do not become dry in summer, both forms would be found. The floating period affords an excellent means for distribution.

When the plants grow upon the soil and are not protected during the winter by a covering of snow or water, they are usually killed by freezing, but in some cases plants which were brown and seemed to be dead produced new thalli from the growing point. The young delicate thalli are well adapted to tide over the dry season, because they can live with a less supply of water than would be needed by the older plants.

RELATIONSHIP OF THE SPECIES.

The form usually described as *Riccia lutescens* should be regarded as a ground form of *Ricciocarpus natans*. Both in the field and in

cultures in the laboratory the forms have been observed showing the transition. There can be no doubt that the plant which I have described is the true *Ricciocarpus natans*, and the description of the ground form as a distinct species came about naturally from the conditions of its growth. In such ponds as have been observed here, the water is high in April and May, so that the floating plants are carried up around the edge and left on the soil. In June or July the water has entirely disappeared from the pond and the only plants found are the slender ribbon-shaped ones which have developed from the floating form. In my first summer's collecting, when the ponds were dry by the last of June, I saw not a vestige of the old *Ricciocarpus natans*, and felt sure that the plants collected were *Riccia lutescens*. It seems possible that the plant was first described as a distinct species from material collected under similar conditions, because it is said to occur in dried up ponds and ditches. If in summer and autumn some water were present, so that some of the typical *Ricciocarpus natans* would be found floating, the origin of the ground form might readily be seen, but in such a case there might be failure to associate the ground form with *Riccia lutescens*. Only by following the development and observing the transition of one form into the other under different conditions of growth can the true relationship be determined. My observations have convinced me that *Riccia lutescens* is only a ground form of *Ricciocarpus natans* and should not be regarded as a distinct species.²

The plant now known as *Ricciocarpus natans* was formerly regarded as a *Riccia*. In the structure of the thallus *Ricciocarpus* is more complicated than the species of *Riccia*. The most important taxonomic characters, however, have been the arrangement of the sexual organs and structure of the sporophyte.

HOOKE first found fruiting plants in dry specimens sent to him by TORREY from New York in 1824. BISCHOFF found fruiting plants in the autumn of 1829 near Heidelberg, and describes antheridial plants, but his figure of the antheridium is not very convincing,

² Having determined the ground form as *Riccia lutescens*, specimens were sent to Professor A. W. EVANS in October 1904. He considered that we were right in referring the plants to that species, but stated the views of different authorities in regard to the status of the species.

as it looks more like the mass of tissue which projects up as a ridge into the median groove, the cells being quite too large for those of an antheridium.

Although HOOKER considered that the plant should remain in the genus *Riccia*, CORDA placed it in a new genus, *Ricciocarpus*, on the basis of HOOKER's description and figures which were taken from dried material. CORDA's figures are copies of HOOKER's. BISCHOFF held that there was no real basis for the change, as the mature sporophyte does not differ from that of other *Riccias*, the separation being based on the mistaken notion that the capsule walls disappear entirely at maturity, and that the genus *Riccia* should not be divided on account of differences in the thallus brought about by the different conditions under which the plant grows, since the method of fruiting is the same in all the species.

LEITGEB regarded *Ricciocarpus* as a distinct genus, on account of the more complex structure of the thallus and the grouping of the sexual organs. He thought that the antheridia were collected into groups similar to those in the Marchantiaceae, but GARBER's results and my own show that LEITGEB was not correct, and that the antheridia actually form only one group. The archegonia are also arranged in a definite part of the plant in one group.

The question now arises whether this is a more advanced condition of development than is found in species of *Riccia*. In the lower species of *Riccia*, the sexual organs are said to be indiscriminately scattered over the surface of the thallus, while in *Riccia fluitans* a regular alternation of single antheridia and archegonia is described. CAMPBELL, in discussing the arrangement of sex organs in *Riccia*, says that in the two forms which he studied, *Riccia hirta* and *Riccia glauca*, he found as a rule that several of one sort or the other would be formed in succession. I have observed the same in *Riccia crystallina*, although the older sporophytes appear scattered in the thallus. LINDENBERG described the fruit of *Riccia crystallina* as scattered, but the antheridia are described and figured as being in a group along the middle part of the thallus. He described and figured the fruit in *Riccia glauca* as being sometimes in rows and sometimes scattered. Most of the figures show them in more or less perfect rows along the longitudinal axis.

In *Riccia minima*, LINDENBERG (20, p. 429) describes and in *pl.* 20 figures the antheridia as arranged in two rows, one on each side of a median groove. In *Riccia bulbosa* the antheridia are along the median groove for its entire length, sometimes in pairs and sometimes far apart. *Riccia Bischoffii* has the antheridia in two or three rows in the thallus.

It seems highly probable that a careful study of a large number of species of *Riccia* by modern methods would show that in many of them there are produced groups of antheridia and archegonia in distinct parts of the thallus.

Since the characters upon which the genus *Ricciocarpus* has been based, with the single exception of the structure of the thallus, have been found wanting, it seems to me that there is not sufficient reason for retaining the genus. The thallus varies in form according to the supply of water, and when growing on the soil has been called a species of *Riccia*. Many plants assume quite different forms when growing under different conditions, but the different forms are not regarded as species.

We should then write:

RICCIA NATANS L. Syst. Veget. 956. 1774.—Bischoff, Nova Acta Acad. Caes. Leop. Carol. 17: 2. 1835.—Lindenberg, Nova Acta Acad. Caes. Leop. Carol. 18:—1836.—Sullivant, Gray's Manual 2ed. 1856.

Ricciocarpus natans Corda, Opiz Naturaliscentausch. 1829.—Leitgeb, Die Riccien, Unters. Lebermoose 4: 1879.—Lindberg, Revue Bryol. 9:82. 1882. (Includes *Riccia natans* L. and *Riccia lutescens* Schw.)—Schiffner, Engler and Prantl. 1893.—Campbell, Mosses and Ferns. 1895.—Underwood, Systematic Botany of North America. Hepaticae. 1895.—Garber, BOT. GAZETTE 37:101-177. *pls.* 9-10. 1904.

Riccia lutescens Schw. Specimen Fl. Amer. Sept. Crypt. 26. 1821.—Lindenberg, Nova Acta Acad. Caes. Leop. Carol. 18: *pl.* 26. 1836.—Sullivant, Mem. Amer. Acad. II. 4: *pl.* 4. 1849.—Sullivant, 2d ed. Gray's Manual 684. 1856.—Underwood, Systematic Botany of North America, Hepaticae. 1895.

Riccia velutina Hooker (in part) Ic. Pl. *pl.* 149: founded on sterile thalli of *Riccia lutescens* and fertile thalli of *Riccia crystallina*, according to Sullivant, Gray's Manual, 1856.

EMBRYOLOGY.

Material for study was collected during the autumn and spring, and fixed very satisfactorily in 1 per cent. chromacetic acid or in chromosmaccetic.

The large air cavities prevent the penetration of the fixing fluid, to overcome which the pieces were submerged by means of cotton plugs. After dehydration the material was passed through chloroform into paraffin. Sections were stained with the triple stain of Flemming or with Heidenhain's iron-alum haematoxylin.

SEXUAL ORGANS.

Young antheridia were found in October. They begin to develop while the plants are young and growing on soil not supplied with a large quantity of water, although the conditions for vegetative growth are good. At this time the thallus is ribbon-shaped, with a thickened apical end and a longitudinal median groove, the thallus in cross-section having about the shape of an inverted Y with a ridge of tissue between the arms (*fig. 9*). Very few plants are found which do not produce antheridia. The archegonia develop later in the same thallus. At first there seemed to be in this a distinction between *Riccia lutescens* and *Ricciocarpus natans*, because *Ricciocarpus natans* has been described by SCHIFFNER, LEITGEB, and CAMPBELL as being strictly dioecious, but the work of GARBER shows conclusively that it is monoecious. The earlier observers state that *Ricciocarpus* fruits in autumn, so it seems probable that their material was collected after the older portion of the plant had decayed, leaving only the portion bearing sporophytes.

The antheridia are produced in acropetal succession in three to five rows (*figs. 10, 11*).

The antheridium develops as has been described for other species of *Riccia*. A superficial cell on the floor of the dorsal furrow just back of an apical cell protrudes above the surface and is cut off by a horizontal wall. The outer cell increases in size, and is divided by three or four cross walls, then a longitudinal wall is formed dividing the young antheridium into two equal parts: this is followed by a second longitudinal wall perpendicular to the first. Then periclinal walls are formed which cut off the single layer of cells which form the wall of the antheridium. The cells in the center now undergo repeated divisions until a very large number of cells is formed. Each of these cells is almost cubical in form and in *Riccia* has been described as producing a single spermatozoid,

KNY (19). The mature antheridium is a short stalked oval body with a conical apex.

As the antheridium develops, the vegetative tissue grows up and surrounds it so that it is enclosed in a cavity which opens into the dorsal furrow. This cavity is formed in the same way as the air spaces of the thallus. The apex of the antheridium is a little below the floor of the dorsal furrow and the sperms escape through the neck formed by the surrounding tissue. Although the antheridia begin to develop in autumn, they are not mature until the following spring, because the growth is checked by the cold. Plants kept in a warm place produced mature antheridia during the winter.

A series of archegonia is developed which is a continuation of the series of antheridia (fig. 7). The archegonium is at first superficial on the floor of the dorsal furrow. Later it becomes enclosed in a cavity by the upward growth of the vegetative tissue as in the case of the antheridium except that the neck of the mature archegonium protrudes above the bottom of the furrow. The origin of the archegonia side by side at the bottom of the dorsal groove is shown in figure 9. In this way three to five rows are formed and later a large number of sporophytes are found in each thallus.

The archegonium develops in general as has been described by JANCZEWSKI (17). My observations confirm the account given by GARBER for *Ricciocarpus natans*, as a comparison of the figures will show, so it is unnecessary to describe the development here.

About the time when the archegonia are mature, cross-sections of the thallus show numerous, delicate, almost hyaline, club-shaped hairs extending up from the floor of the median groove. Each hair consists of a stalk of two or three short, narrow cells with a much larger cell at the free end. These hairs bear a striking resemblance to paraphyses (fig. 78). LEITGEB (22, p. 31) describes "papillae" which grow up from the bottom of the groove and regards it as highly probable that it was the dried remnants of these which LINDENBERG observed when he wrote: "Sporangium vor aussen mit kleinen unregelmässigen braunen Schuppen bedeckt ist, die Fragmente einer zersprengten früheren Hülle zu sein scheinen." As the hairs become older they become brown and break down so that they

would give much the appearance described by LINDENBERG. We know now that the sporophyte has no *Hülle* or sheath.

SPOROPHYTE.

The development of the sporophyte agrees with the account given by CAMPBELL (3) for *Riccia* and by GARBER for *Ricciocarpus natans*.

The first division is usually transverse but may be oblique (*fig. 21*). The next wall may be perpendicular to the first so as to form a quadrant (*fig. 22*), or parallel to it, producing a row of cells. Divisions take place in all directions after this until an almost spherical mass containing several cells is formed. Then the amphithecium becomes distinct as a single layer of cells enclosing the spore producing cells. The growth takes place rapidly but the divisions of the cells are not simultaneous, usually only a few dividing cells being found in a sporophyte.

The sporophyte continues its growth until a solid mass of three to four hundred cells is produced. Then the calyptra and amphithecium expand and the spore mother-cells becoming free separate from one another and become rounded. From the surrounding cells, which are richly stored with food, there is secreted a large amount of nutritive material which fills the space around the mother-cells, giving them favorable conditions for growth (*figs. 25, 26*). The spore mother-cells increase rapidly in size and again fill the cavity. That part of the nutritive material not absorbed by the spore mother-cells is pressed into thin plates between them. This material takes a deep blue stain with gentian violet. A fuller discussion of the spore mother-cells and of their division to produce the spores will be given in another place.

Before the spores are mature the inner layer of the calyptra collapses. The amphithecium is distinguishable until the spores are almost mature. The outer layer persists but the cells are usually shrunken. The contents of these cells is no doubt used up to supply the growing spores with nourishment. All of the spore mother-cells produce spores, there being no sterile tissue in the form of elaters. In discussing the simple form of sporophyte of *Riccia*, GARBER considers that the absence of sterile tissue is to be associated with the habit of the plants; since there is not much chance for the attachment of an independent sporophyte, there is no sterile tissue in

the form of a foot. When we consider the fact that some other Hepaticae which have the foot well developed grow on very wet soil and require as much moisture for their development as do some of the species of *Riccia*, this theory does not seem entirely convincing.

The sporophyte develops during May and June. A given sporophyte requires about three weeks for its development.

SPOROGENESIS.

Usually the most favorable cells for the study of cytological details are the spore mother-cells. Their large size, abundant contents and active growth at the time when divisions are taking place, permit good results in fixation. *Riccia crystallina* has furnished the most satisfactory material.

In July, 1903, an abundance of fruiting *Riccia crystallina* was found growing on the mud on the bottom of a dried up pond not far from the ponds where the form known as *Riccia lutescens* was growing. This species had never been collected in this region before. Having so determined the plant, I referred specimens to Prof. A. W. EVANS who confirmed my determination. He says: "Apparently this species represents an addition to the hepatic flora of New York. I find no mention of it in local lists of New York plants and there are no specimens of it from your state in my herbarium."

These plants had been growing under favorable conditions, as the pond had not contained much water at any time during the spring. The thalli formed rosettes growing so close together as almost to cover the ground. The number of fruiting plants was very striking, as it seemed impossible to find a single sterile plant. All stages in the development of the sporogonium and spores were easily obtained, and some stages in the development of the sexual organs, but changes were taking place very rapidly and the younger stages were of comparatively rare occurrence. The development of the sexual organs and fruit agrees with that of other species of *Riccia*. Each thallus produces several sporophytes which are easily recognized when mature as small black spherical bodies imbedded in the tissue.

These plants continued to develop and produce sporophytes for only a short time after they were discovered. The month of July

was the most favorable time for the collection of material showing karyokinesis in the spore mother-cells. During August, the spores became mature and the thalli broke down. No good specimens could be collected after August 25. This differs from what has been observed for some other species of *Riccia*, which are described as withstanding long periods of drought, the thalli continuing their growth again when supplied with moisture. (CAMPBELL, 3.)

During the following winter this pond became filled with water and did not become dry until late in the summer, so that only a few plants were found as compared with the large number of the preceding year. This made a difference in the time of fruiting. In September the sporophytes were in about the same stage of development as in July of the preceding year. This may explain why different authors give different seasons for the fruiting of *Riccia*. It seems that conditions of temperature and water supply exert such an influence that in the same species and locality the time may vary considerably from year to year. In general, I think it may be said that good conditions for vegetative growth will hasten rather than retard the fruiting of *Riccia*.

The thallus of *Riccia crystallina* is small and thin; its surface presents a series of wide depressions separated by thin lamellae; and there are no ventral scales. The fixing fluid easily penetrates and the spore mother-cells are usually well fixed.

The development of the spore mother-cells agrees with the account given for *Riccia natans*, but there is not such a large number produced in a sporogonium. When the spore mother-cells come to lie loosely in the sporogonium, they are surrounded by nutritive material. The mature spore mother-cells are then generally spherical, but they may be elliptical or so angular by crowding as to look like a tissue. The contents of the spore mother-cells of *Riccia* has been described as granular by CAMPBELL (3) but the structure of the cytoplasm in *Riccia crystallina* is a fine reticulum with the granules occurring usually at points of intersection of the fine threads of the network. The older spore mother-cells as well as the mature spores contain considerable oil.

In the nucleus of the spore mother-cell the chromatin is scanty and is irregularly scattered on a fine linen network. No nucleolus

has ever been observed (*fig. 34*). When the nucleus is preparing for division, the chromatin leaves the linin network and collects into several bodies which soon move together to form one irregular mass. I regard this as the synapsis stage. Such bodies of chromatin have been found often and in cells which seemed to be well fixed so it seems to represent a stage in the preparation for division and not to be a result of shrinkage as has been suggested by certain authors for other plant cells in which the same condition has been observed. The body of chromatin occupies a position at one side of the nucleus, and the rather large nuclear cavity appears hyaline. There can be little doubt that the body described by CAMPBELL (3) as a nucleolus is really the entire mass of chromatin in the synapsis stage.

From this mass of chromatin a short thread develops which later segments to produce the chromosomes (*fig. 35*). The small amount of chromatin present here makes the details very difficult to determine. The four chromosomes, easily counted here as well as in the nuclear plate and on the way to the poles, are very small and appear almost spherical when on the spindle although they are short, thick, curved rods.

The development of the spindle is not easily observed. Divisions take place almost simultaneously in all the cells of a sporogonium and the changes are very rapid. By far the commonest stage of division is that in which the chromosomes are in the nuclear plate (*fig. 38*). Neither centrosomes nor centrospheres occur in the spore mother-cells of either *Riccia crystallina* or *Riccia natans*. Around the nucleus preceding the formation of the spindle, there is an accumulation of material, apparently composed of fine fibres. The nucleus elongates, becoming somewhat elliptical but not sharp pointed. The fibres about the nucleus do not give the appearance of centrospheres but are like the web of kinoplasmic fibres described for certain pollen mother-cells (*figs. 36, 37*). It has been impossible to find any nucleus which showed anything resembling a multipolar spindle. The poles of the spindle are probably determined by the elongation of the nucleus at an early stage in the spindle formation. The spindle is composed of very fine fibres, some of which extend from pole to pole, while others extend from the poles into the cytoplasm, reaching almost to the nuclear plate (*fig. 38*). The

mature spindle has very broad poles and its formation does not seem to have been controlled by a centrosome or a centrosphere, as a comparison of the spindles of the spore mother-cells with those of the cells of the antheridium makes clear.

The minute chromosomes separate, four going to each pole, after which a cell plate is formed in the usual way (*figs. 40, 41*). The daughter nuclei do not come to a true resting stage. The chromatin is scattered in almost spherical bodies in the hyaline cavity of the nucleus, which do not represent the individual chromosomes, as their number and size vary considerably (*fig. 42*).

The second division takes place in much the same manner as the first. The spindles are arranged with their long axes parallel to the first cell plate, so that the cell plates formed in these spindles are almost perpendicular to that formed in the first division (*figs. 43-47*). The latter does not disappear during the second division but remains and the walls separating the spores are laid down here (*fig. 47*). The walls separating the cells of the young tetrad are thin and delicate, but in the mature spore the outer layer of the wall becomes thickened and folded. The mature spore is almost black, and its contents are largely oil. When carried through chloroform into paraffin and sectioned, the spores seem to have only scanty granular contents, due to the fact that the oil has been removed in the process. The nucleus is very small.

During the winter and spring following their development, unsuccessful attempts were made to germinate the spores. It may be that they had been allowed to remain dry too long before they were moistened, for in nature they would not be dry very long even in tiding over a dry season.

The spore mother-cells of *Riccia natans* do not furnish such satisfactory material for study as do those of *Riccia crystallina*, because the large air cavities of the thallus prevent the penetration of the fixing fluid and so the spore mother-cells often shrunk. A sufficient number of good preparations was secured, however, to show that the process of division does not differ from that of *Riccia crystallina*.

SPERMATOGENESIS.

The development of the spermatozooids has been treated by a number of investigators, among them, CAMPBELL (4), LECLERC DU SABLON (23), GUIGNARD (14), SCHOTTLANDER (27), and STRASBURGER (29). It will be observed that most of these papers were published before methods of preparing material for study were so well developed as at present. The work of BELAJEFF (1) confirmed by that of STRASBURGER (29) shows that the spermatozoid in the Hepaticae consists not only of the metamorphosed nucleus but also of the cytoplasm.

IKENO (16) not only confirms the view that the spermatozoid consists of cytoplasm as well as nucleus but also discusses the development of the cilia and the homology of the blepharoplast and centrosome of *Marchantia polymorpha*.

He finds that the body which becomes a blepharoplast in the developing spermatozoid appears in the earlier nuclear divisions of the antheridium and functions as a centrosome. It is, however, not permanent, but appears at the time of nuclear division and disappears during the process, so that it is not found in the daughter cells until about the time for the formation of the spindles of their division. After the last division which gives rise to the cells that develop into the spermatozooids, the body does not disappear but remains and becomes a blepharoplast. IKENO argues from this that the centrosome and blepharoplast are homologous. He has good grounds for such an argument in the case of *Marchantia polymorpha*, because centrosomes have been reported also in the vegetative cells of that plant, by MOTTIER (24) and by VAN HOOK (32). In other plants which have the blepharoplast, centrosomes are not found, and the body appears in only one or two divisions before the formation of the cells which produce the spermatozooids.

MOTTIER (26) in discussing IKENO's paper raises the question whether the bodies which IKENO has figured as centrosomes are in some cases more than ordinary granules such as appear in the cytoplasm of other cells in which centrosomes are known to be absent. IKENO has pointed out, however, that the cytoplasm of these cells is very finely granular, there being no other bodies in the cell which bear any resemblance to the ones figured as centrosomes. He also calls

attention to the fact that centrospheres have been described in dividing spore mother-cells of *Pellia epiphylla*, by FARMER (6, 7, 8, 10) and by DAVIS (5). The occurrence of centrospheres here has been questioned, however, by GRÉGOIRE (13). In a recent paper, FARMER (9) reports centrospheres and occasional centrosomes in the spore mother-cells of *Aneura pinguis*.

In order to get good results in *Riccia natans* it is necessary to fix the material when growing rapidly. About equally good results were secured with chromacetic acid and with Flemming's weaker solution. The sections were stained with anilin safranin and gentian violet. It was found best to stain deeply in gentian violet and then to wash out carefully. In this way all details can be brought out clearly, although IKENO did not find it good for Marchantia.

The development of the antheridium has been described. When almost mature it consists of a large central mass of cubical cells surrounded by a wall one cell in thickness (fig. 33). In preparations from plants in which some antheridia are mature, one finds several stages in the development. The nuclear divisions do not take place simultaneously throughout an antheridium but usually all the cells of one of the segments marked out by the first walls dividing the antheridium, show the nuclei in the same stage of karyokinesis. In the most favorable preparations, therefore, one may find several stages of division in the same antheridium.

The cells of the young antheridium are almost cubical, with finely granular cytoplasm. The nucleus is rarely exactly spherical and has a rather thick membrane. The chromatin is in an irregular central mass, made up of a number of pieces. A nucleolus cannot be distinguished. The cavity surrounding the chromatin is large and hyaline (figs. 53, 54). In some cases a large number of small bodies of chromatin were found scattered irregularly in the nuclear cavity. The number of chromosomes is four. It seems that the nuclei in the young rapidly growing antheridium rarely come to a typical resting stage.

The question of the presence or absence of centrosomes in the cells of the young antheridium was taken up carefully, because previous observations on the karyokinetic figures in the sporophyte cells and spore mother-cells have convinced me that no such bod-
AI

appears there. On the other hand centrosome-like bodies appear in the cells of the older antheridia at the time of nuclear division. There can be no doubt that these are distinct bodies, and they cannot possibly be interpreted as accidental granules in that position. In some of my preparations hundreds of cells showing them are found on a single slide, and they are so distinct that the preparation could easily be used for class demonstration. These bodies appear in the cells of the antheridium in early stages of its development. I have been unable to determine whether they appear in the earliest cell divisions but they appear in the antheridia which consist of only a few cells. They are not permanent, but disappear and arise anew with each division.

IKENO regarded it as highly probable (though unable to state this positively) that in *Marchantia* these bodies were of nuclear origin. He figures a small spherical body inside the nuclear membrane, which in a later stage is found outside the membrane. This body then divides into two, which arrange themselves on opposite sides of the nucleus. If the bodies have their origin as one, which later divides as described, they act as do the centrosomes which have been described for other plants.

In *Riccia natans*, nothing has been observed to indicate that the body is of nuclear origin, except that it stains in much the same way as the mass of chromatin in the nucleus. In some of my preparations a single body has been observed near the nuclear membrane (fig. 53). These bodies have never seemed so distinct as the ones which appear at the opposite ends of the nucleus and in the poles of the spindle. There is a dark central part, surrounded by a mass of cytoplasm which is more or less irregular but does not give the appearance of distinct radiations such as are described in the centrospheres of certain plants.

When these single bodies were discovered, a careful search was made of the same preparations and of others in which the two bodies were on the opposite sides of the nucleus, in order to discover if possible the intermediate stages which it would seem should appear in such preparations. In cases in which two bodies have been observed, they have always been on opposite sides of the nucleus, or so nearly opposite that the spindle developing between them

might take the curved form shown in *fig. 60*. The origin of the two bodies is of importance in determining the homology of the centrosome and blepharoplast and will be discussed later.

Starting with the stage in which the centrosome-like bodies are on opposite sides of the nucleus, the nuclear division takes place in the following manner. At first the bodies are at a little distance from the nuclear membrane, then the nucleus elongates so that the membrane closely approaches the bodies, becoming somewhat pointed. At the same time one observes that there is a collection of kinoplasm at the poles of the nucleus and extending along the nuclear membrane for some distance. At this time the bodies at the poles do not show radiations in any direction, but are very distinct (*fig. 54*). The spindle is formed from the kinoplasm which has been described, and when formed consists of a few thick fibres which converge at the poles, so that the centrosome-like bodies occupy the position of true centrosomes. About the time when the spindle develops, the chromosomes are formed from the central mass of the nucleus and become arranged in the nuclear plate. They are closely crowded together in this stage, and not so easily counted as when they have moved to the poles. The photograph (*figs. 75, 76*) shows the dense mass formed by the chromosomes when arranged in the nuclear plate. It was impossible to determine how the division takes place in the chromosomes as they move to the poles. The changes take place so rapidly that stages are rarely found in which the chromosomes are on their way to the poles.

The centrosome-like bodies disappear during the division, but it is difficult to say at just what point. *Fig. 56*, a cell taken from an antheridium in which only one or two more divisions will take place, shows the centrosome-like bodies quite distinctly when the chromosomes are almost at the poles, but by the time the chromosomes are at the poles and before the daughter nuclei are formed, the bodies disappear (*fig. 57*).

These bodies are best seen in preparations which have been over-stained and washed out. In some cases my preparations were stained deeply enough to show the spindle and chromosomes well, but only an occasional spindle showed the bodies at the poles. When these slides were over-stained and carefully washed out, the bodies were brought out very distinctly in all cases.

After a large number of divisions has taken place the antheridium consists of nearly cubical cells, each of which has been considered by earlier investigators to produce a single spermatozoid. STRASBURGER (30, p. 482) says of *Marchantia polymorpha*: "Die Spezialmutterzellen der Spermatozoiden sind durch fortgesetzte, sich rechtwinklig schneidende Teilungsschnitte angelegt worden." CAMPBELL (4) describes and figures the spermatozoid mother-cell of *Pellia* as producing two spermatozooids. IKENO (16) discovered that in *Marchantia* each of the cubical cells undergoes another division in which the spindles are arranged diagonally, in the earlier divisions the long axis of the spindle being parallel to the long axis of the cell. In this last diagonal division no cell wall is formed between the daughter cells, each of which develops into a spermatozoid. Thus each of the cubical cells produces two spermatozooids instead of one. IKENO cites several cases in which two spermatozooids are produced from a single mother-cell and thinks that this is probably general in the liverworts and mosses.

JOHNSON (18) has described a diagonal division of the cubical cells of *Monoclea*, but he figures a wall separating the two parts of the cell and regards each three-cornered cell as the mother-cell of a spermatozoid. He does not give the details of nuclear division in the earlier stages of the antheridium nor in the formation of the spermatozoid mother-cells.

In the last division of the cells in the antheridium of *Riccia natans* the spindles are arranged diagonally as in *Marchantia*. This arrangement of the spindles is quite striking. They are larger than in the earlier divisions and the bodies at the poles are very distinct. In some cases the spindles are curved (figs. 58-60).

No wall is formed between the daughter cells, each of which develops into a spermatozoid. The centrosome-like bodies do not disappear after this division (fig. 61). They remain in the cells, at first near the nuclei. The daughter cells are contracted, occupying the central part of the cell cavity (figs. 62, 63). Soon the centrosome-like body moves away from the nucleus toward the end of the cell. Those in the two spermatids may be at the same end or at opposite ends (figs. 63-67). When the spermatid has become somewhat rounded, the centrosome-like body has taken its position in contact

with the cell membrane (*fig. 68*). When the cilia appear they are inserted in this very small body so that it comes to function as a blepharoplast. Its small size as compared with that of the cilia of the mature sperm makes it seem probable that some of the material for the growth of the cilia must be drawn from another source than the blepharoplast itself, although it disappears to such an extent that in the mature sperm it cannot be recognized as the point of insertion of the cilia.

The developing spermatozoids of *Riccia natans* do not remain enclosed in the mother-cells until they are mature, but at about the stage represented by *figs. 70, 71* the walls break down and the young spermatozoids lie free in the cavity of the antheridium. Here they seem to undergo considerable growth. The material for this growth is probably derived from the surrounding cells as they become collapsed in old antheridia.

The nucleus of the developing spermatozoid takes a position at one side of the cell and becomes homogeneous. It seems probable that other material than the chromatin of the spermatid nucleus must enter into this part of the spermatozoid, because it is very evident that the body contains more material than would be obtained from the chromatin alone. Soon the nucleus elongates, following the outline of the cell and becoming crescent-shaped (*figs. 71-73*). In some cases, a distinct vacuole occurs in the cytoplasm although this is not always the case (*figs. 71, 72*). The mature spermatozoid becomes long and slender and consists of the nucleus, the material of which seems to have increased in amount, a small amount of cytoplasm, and the cilia which are derived from the blepharoplast and in all probability from a part of the cytoplasm surrounding it. IKENO describes a spherical body which appears in the spermatids of *Marchantia* before the cilia begin to develop and disappears about the time that changes take place in the nucleus. It has been impossible to find such a body in *Riccia*, although it would seem, judging from IKENO's figures, that it could easily be seen if present.

The question of the homology of the blepharoplast and centrosome is one which it seems to me has not yet been settled. In *Marchantia*, where centrosomes have been reported in the vegetative cells as well as in the antheridium, the evidence seems good that the

centrosome and the blepharoplast are homologous, and this is the conclusion of IKENO. In all other plants in which blepharoplasts are known to occur, centrosome-like bodies are not present in any cell divisions except those immediately preceding the formation of the sperms. That centrosomes occur in liverworts in cells outside the antheridium is open to question. The conflicting reports of those who have investigated *Pellia epiphylla* make it clear that no distinct body occurs there which can be regarded as a centrosome, although aggregations of kinoplasm, called centrospheres by most authors, do occur.

In *Riccia natans*, it seems very evident that centrosomes do not occur in the divisions of the spore mother-cells. The spindle poles are broad, and there is not even a suggestion of a centrosphere such as has been described for *Pellia*. In the cells of the sporophyte GARBER reports centrospheres but no centrosomes. I have never been able to observe them in my preparations. When the spindle is fully formed there are no fibres radiating into the surrounding cytoplasm (*figs. 48-52*).

Although the thallus of *Riccia natans* does not present favorable material for cytological study, a number of cells showing nuclear division in the gametophyte have been observed near the growing point. The greatest difficulty here is the presence of numerous deeply staining granules in the cell. In some cases granules resembling centrosomes appear at the poles of the spindle, but they do not differ in appearance from the other granules of the cell, and it seems probable that their occurrence here is accidental.

Summing up, we find that in *Riccia natans* centrosomes are not found in the cells of the gametophyte, sporophyte, or spore mother-cells, but that bodies occur in the dividing cells of the antheridium which seem to function as centrosomes. In *Riccia* and *Marchantia*, the blepharoplasts certainly have much more the appearance of centrosomes than in any other plants in which blepharoplasts have been described. The bodies have every appearance of centrosomes when at the poles of the elongated nucleus or at the poles of the spindle. Perhaps the strongest objection to regarding these bodies as centrosomes lies in the fact that in *Riccia natans* they occur only in the cells of the antheridium, while the blepharoplasts reported

in other plants appear only in the last two generations of cells concerned in the formation of spermatozoids.

Those who argue in favor of the homology of the centrosome and blepharoplast certainly find their best evidence so far in the liverworts, but it seems to me that this evidence is not conclusive when the bodies occur only in cells of the antheridium.

In those plants in which centrosomes are known to occur, a single body divides to produce two, which arrange themselves on opposite sides of the nucleus (MOTTIER, 25). IKENO has reported a similar condition in *Marchantia*. In *Riccia natans*, however, the evidence seems to favor the view that the two bodies arise anew with each division, appearing on opposite sides of the nucleus at the same time. In this respect they behave more like blepharoplasts.

MOTTIER (26) in discussing this question has called attention to the fact that it is questionable whether we can speak of organs as homologous which, as such, are without genetic continuity. The question as to whether true centrosomes have genetic continuity has not yet been decided, but it is probable that they do not in all cases.

SUMMARY.

1. *Riccia lutescens* and *Ricciocarpus natans* are forms of the same plant, the former occurring on the ground in summer and autumn when the ponds are dry, and the latter as a floating form. Either form can be changed into the other by altering the supply of water. Therefore, *Riccia lutescens* should not be regarded as a distinct species.

2. The genus *Ricciocarpus* has been based largely on characters which do not exist. In my opinion, the only real basis for separating it from *Riccia* is the more complex structure of the thallus. BISCHOFF did not regard this as a good character for the separation of the genus.

3. The plant is monoecious, antheridia and archegonia being produced in definite groups in the same thallus. The sexual organs appear in autumn when the thalli are growing on the ground and complete their development the following April. Abundance of water is not essential to sexual reproduction, as the plants fruit when kept growing on the soil and supplied with a limited amount of

water; therefore the ground form is not sterile, as was the opinion of LINDBERG and GARBER.

4. Plants which have been growing attached to the soil and have been submerged by the filling up of the ponds do not necessarily perish, but are adapted to spend the winter under water and then to break loose by the decay of the older part of the thallus and float upon the water in the spring.

5. The plants are propagated vegetatively by the separation of branches of the thallus, by the decay of the older part, and also by the growth of new plants from cells in the apical region.

6. The sexual organs and fruit of the two species studied agree in their development with the accounts given for the other species of *Riccia*. There is no rudimentary integument surrounding the archegonium or sporophyte of *Riccia natans*. The sporogonium of *Riccia natans* is larger than that of *Riccia crystallina* and produces a larger number of spores. The only sterile tissue in either is the amphithecium, a single layer of tabular cells surrounding the mass of spore mother-cells.

7. Centrosomes are not present in cells outside the antheridium nor would I interpret any structure observed in the cells of the sporophyte or the spore mother-cells as a centrosphere.

8. Bodies which resemble centrosomes, and which are considered to be true centrosomes by certain authors, occur in the cells of the antheridium. These bodies do not have genetic continuity, but arise *de novo* with each division. They do not disappear after the last division of antheridial cells but remain in the spermatids and later become blepharoplasts.

9. In the earlier divisions of cells in the antheridium, the spindle is arranged parallel to the long axis of the cell, but in the last division, the spindle is placed diagonally in the cell. No wall is formed between the two cells produced by this division, each of which becomes a spermatozoid. Thus two sperms are produced from each cuboidal cell.

10. In the developing sperm, the blepharoplast takes a position on the membrane of the cell and the two cilia grow from it, the nucleus becomes almost homogeneous in structure and crescent-shaped, almost enclosing the cytoplasm. The mature sperm consists of the

nucleus, the cytoplasm, and cilia which have received material for their growth from the blepharoplast and probably also from the material surrounding it.

11. The amount of chromatin in the nucleus is small. There is no nucleolus present unless the masses of chromatin which are found in nuclei which are undergoing repeated division be interpreted as nucleoli.

12. The number of chromosomes is four for the gametophyte and eight for the sporophyte.

13. The cytoplasm of the spore mother-cells appears to be a fine reticulum, in which are numerous granules usually located at the point of intersection of the fibres of the reticulum.

14. The mature spore contains a large quantity of oil together with a small amount of granular matter. The nucleus of the spore is very small.

In conclusion I wish to thank Professor GEO. F. ATKINSON and Dr. E. J. DURAND for valuable advice and assistance during the progress of this study.

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EXPLANATION OF PLATES V-IX.

All drawings, except *fig.* 7, were made with camera lucida. *Figs.* 8-52, with Bausch & Lomb oculars and objectives, as follows: *Figs.* 8, 10, 11, 1 in. ocular, $\frac{2}{3}$ objective; 9 and 25 2 in. oc., $\frac{1}{8}$ obj.; 19, 21-24, 26, 32, 33, 2 in. oc., $\frac{1}{2}$ obj.; 12-18, 20, 27-31, 34-52, 1 in. oc., $\frac{1}{2}$ obj.; *Figs.* 53-73 with Zeiss oc. 18, 2^{mm} apochromatic objective, 1.40 aperture.

The figures of plate VI were reduced slightly more than one-half in reproduction.

All figures are of *Riccia natans* except the spore mother-cells (*figs.* 34-47) which are of *Riccia crystallina*.

PLATE V.

FIG. 1. Rosette of plants growing on the soil; *a*, natural size; *b*, enlarged.

FIG. 2. Land plants growing in regular clusters.

FIG. 3. Two plants growing on soil, one of which has been injured and has grown out in an irregular way from the growing point.

FIG. 4. New plants growing from apical cells of old thalli.

FIG. 5. *a*, Decay of older part of thallus of the land form to give the floating form; *b*, plants collected in May. If these thalli should become stranded on the mud and growth should continue rosettes would be formed.

FIG. 6. Plants decolorized in alcohol. The sporophytes appear as chains of dark bodies in the thallus.

PLATE VI.

FIG. 7. Longitudinal section of thallus parallel to the dorsal furrow, showing arrangement of sexual organs.

FIG. 8. Cross-section of thallus showing archegonia.

FIG. 9. Cross-section of thallus, showing the origin of archegonia in rows on floor of dorsal groove.

FIG. 10. Cross-section of thallus, antheridia.

FIG. 11. Longitudinal section of thallus parallel to surface, showing the arrangement of antheridia. Archegonia have not begun to develop.

FIGS. 12-18. Stages in development of archegonium.

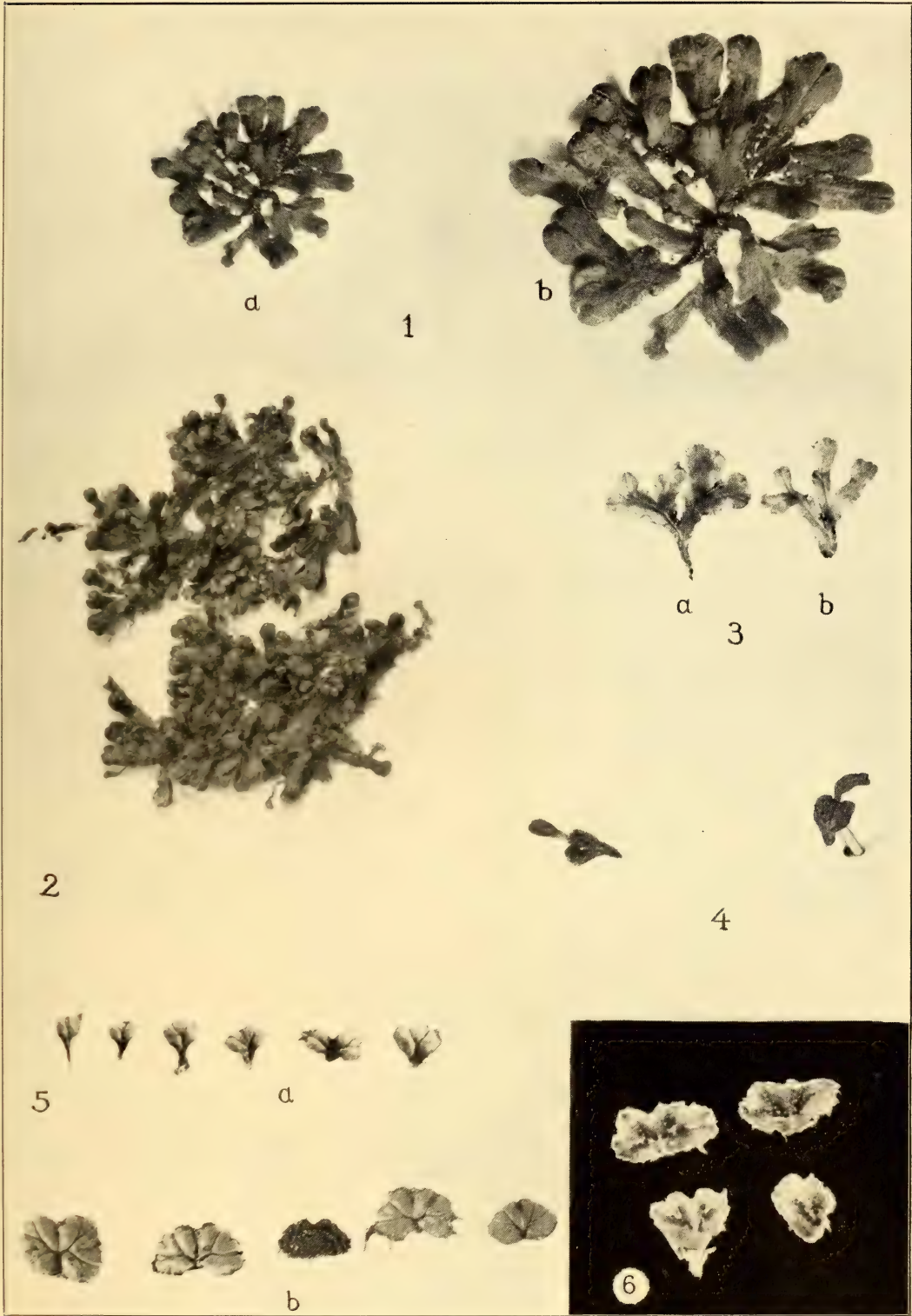
FIG. 19. Archegonium in which egg-cell has not been fertilized and is shrunken.

FIG. 20. Cross-section of neck of archegonium.

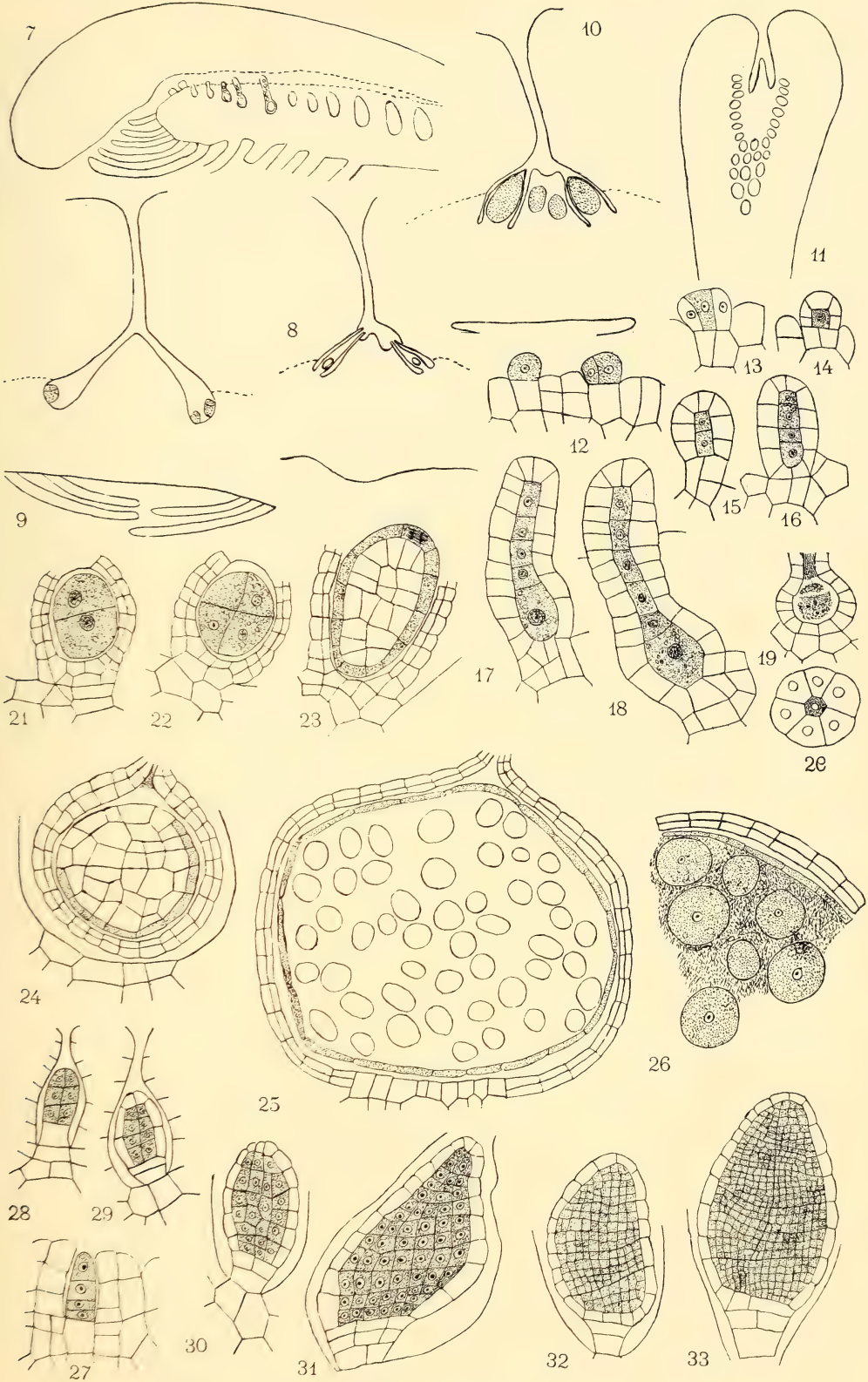
FIG. 21-25. Stages in development of sporophyte.

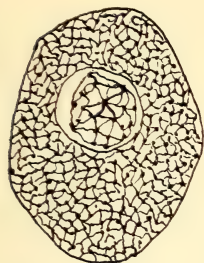
FIG. 26. Spore mother-cells.

FIGS. 27-33. Development of antheridium. *Figs.* 27-31, from material collected in October.

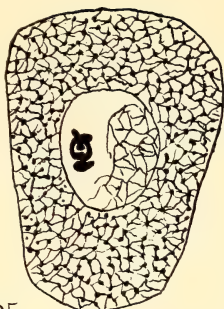


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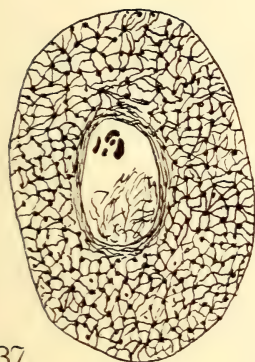
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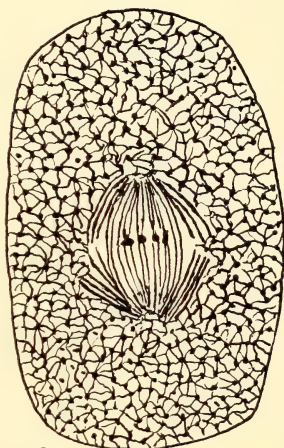
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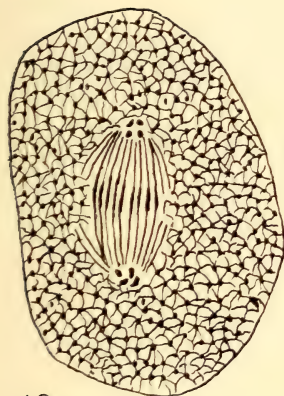
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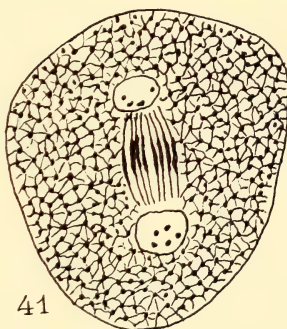
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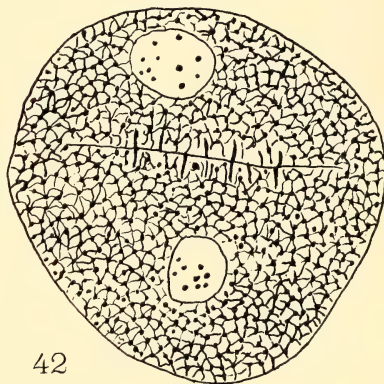
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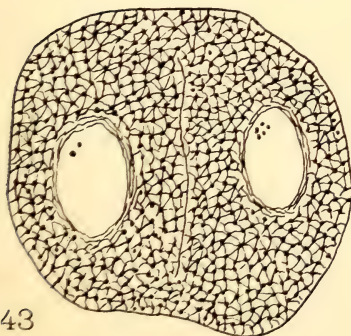
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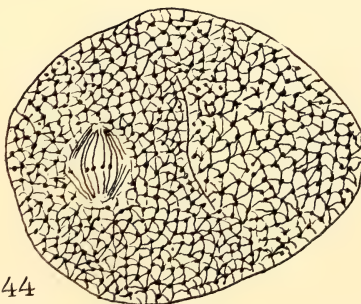
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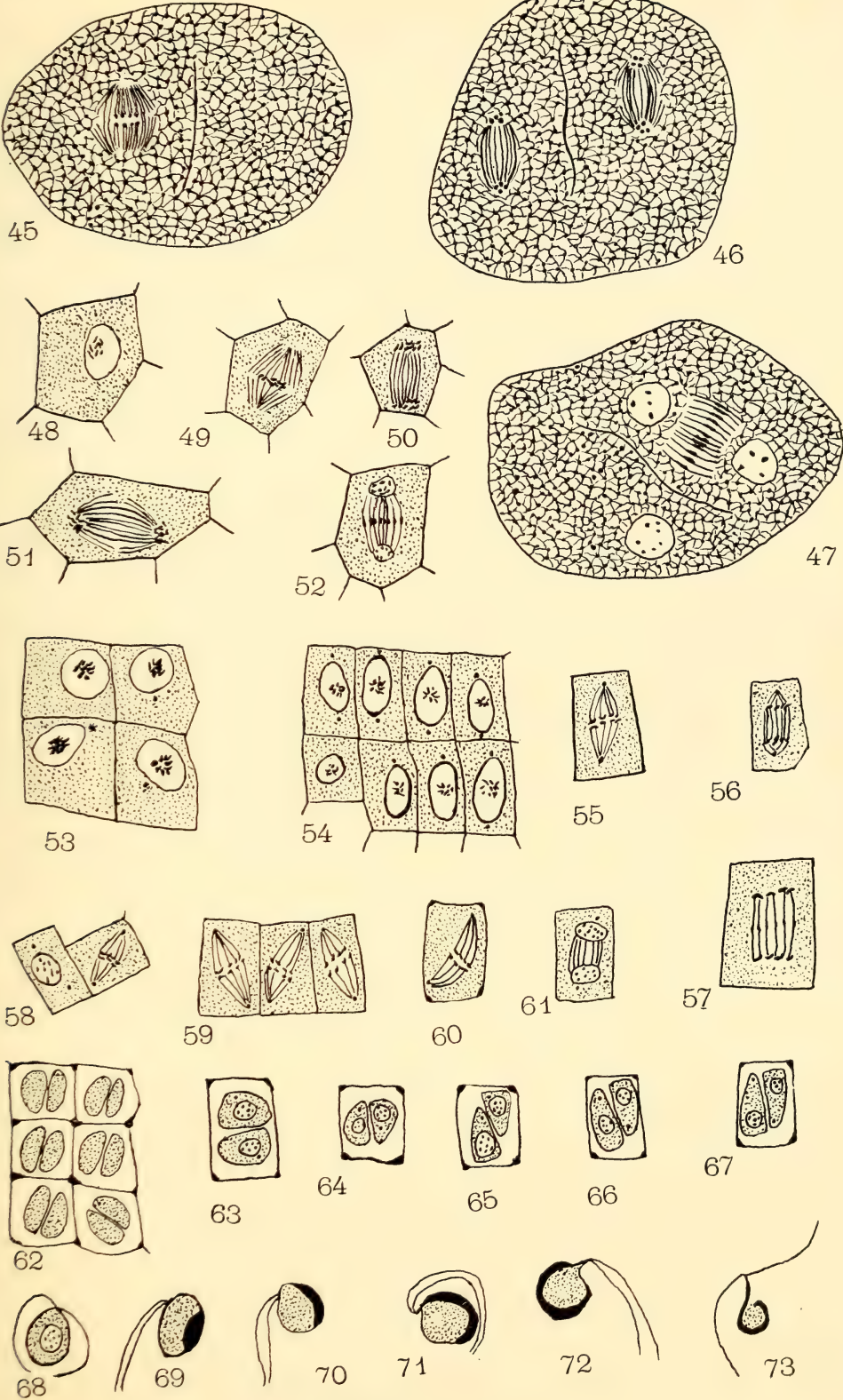
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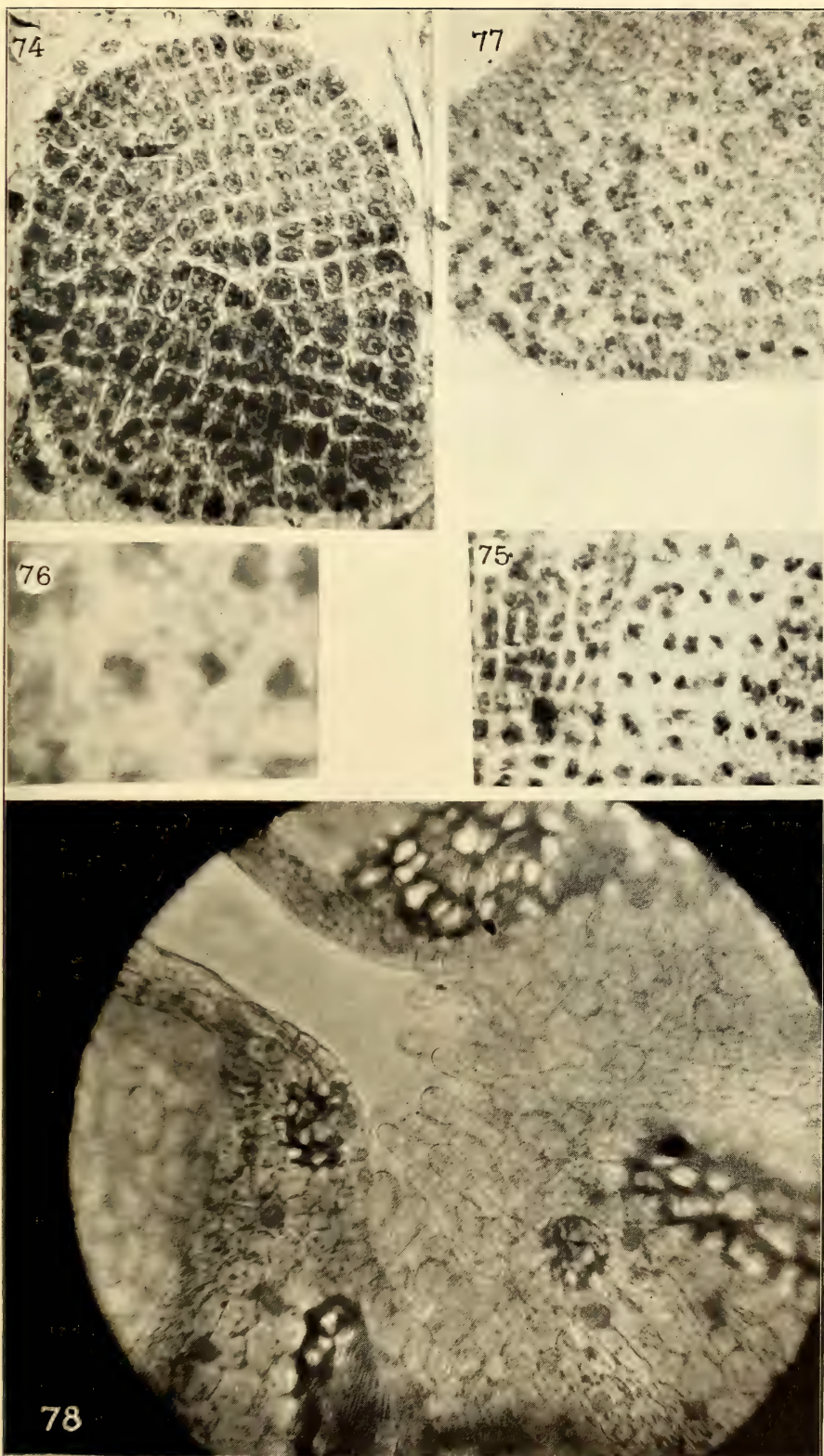


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PLATE VII.

FIG. 34. Spore mother-cell in resting state. Chromatin on a fine linin network.

FIG. 35. The chromatin is in the form of an irregular thread.

FIG. 36. Chromosomes formed; web of delicate fibres about the nucleus.

FIG. 37. Nucleus elongated and showing a web of fibres.

FIG. 38. Spindle with chromosomes in place. No centrosome.

FIG. 39. Chromosomes moving to poles of spindle.

FIG. 40. Chromosomes at the poles, thickening of spindle fibres to form cell plate.

FIG. 41. Daughter nuclei.

FIG. 42. Cell plate. Daughter nuclei contain numerous spherical bodies of chromatin which stain bright red with safranin.

FIG. 43. Daughter nuclei preparing for division.

FIG. 44. Daughter nucleus with chromosomes in place. Neither centrosphere nor centrosome.

PLATE VIII.

FIG. 45. Chromosomes moving to poles.

FIG. 46. Daughter nuclei with chromosomes at the poles to form nuclei of spores. The cell plate formed in the first division persists.

FIG. 47. Second division completed.

FIGS. 48-52. Stages in the division of a sporophyte cell. No centrosome. *Fig. 48* shows slight radiation of cytoplasm from the poles of the elongated nucleus.

FIG. 53. Cells of antheridium which show a single rather irregular body near the nucleus.

FIG. 54. Cells of antheridium which shows the distinct centrosome-like bodies at the poles of the elongated nuclei. Compare *fig. 74*.

FIG. 55. Spindle with centrosome-like bodies at the poles.

FIG. 56. Centrosome-like bodies present when the chromosomes are almost at the poles.

FIG. 57. Cell from young antheridium. Chromosomes at poles. No centrosome can be distinguished.

FIG. 58. One cell preparing for last division, while the adjoining cell has the spindle formed and arranged diagonally.

FIG. 59. Diagonal arrangement of spindles in last division of cells in the antheridium.

FIG. 60. Curved spindles.

FIG. 61. Daughter nuclei formed after diagonal division; centrosome-like bodies present.

FIG. 62. Cells of antheridium after last division.

FIGS. 63-67. Spermatids in mother-cells.

FIGS. 68-73. Stages in the development of the spermatozooids.

PLATE IX.

FIG. 74. Antheridium in which the nuclei are elongated and preparing for division.

FIG. 75. Portion of section of an antheridium showing the spindles with the dense chromosomes in the plate and in some cases the centrosome-like bodies at the poles.

FIG. 76. Two cells of the same section enlarged three times.

FIG. 77. Chromosomes at the poles of the spindles.

FIG. 78. Cross-section of thallus showing the hyaline hairs which extend up into the median grooves.

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